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STUDIES ON THE LIFE HISTORY OF TWO CORAL-EATING NUDIBRANCHS OF THE GENUS *PHESTILLA*

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This report describes the results of studies on the life history of two tropical coral-eating nudibranchs of the aeolid genus *Phestilla*. *Phestilla melanobranchia* Bergh, 1874, feeds primarily on ahermatypic corals in the Family Dendrophylliidae; *Phestilla sibogae* Bergh, 1905, feeds on hermatypic corals in the Genus *Porites*. Both species were reared through their entire life cycle in the laboratory.

Adult morphology is strongly emphasized in the taxonomic literature on nudibranchs but little information is available about such aspects as egg mass and veliger morphology (Hurst, 1967), factors influencing metamorphosis (Harris, 1973), growth and fecundity rates and longevity (Miller, 1962 and Thompson, 1964). The egg mass of *Phestilla sibogae* was described by Kawaguti (1943) and Ostergaard (1950). Bonar (1973) and Bonar and Hadfield (1974) have given detailed descriptions of morphological and ultrastructural changes during metamorphosis in *Phestilla sibogae*.

Attempts to cultivate different developmental types have been summarized by Hadfield (1963), Thompson (1967) and Harris (1973). To date only two nudibranch species with a planktotrophic veliger stage have been reared through metamorphosis. K. Engel (personal communication, 1971, University of California at Santa Barbara) raised the aeolid *Hermissenda crassicornis*, and the development of *Phestilla melanobranchia* is described below.

Providing the factor or factors necessary to induce metamorphosis is a key criterion for the successful cultivation of nudibranchs. The factors influencing metamorphosis fall into two categories (Harris, 1973). In all cases reported, a host factor or chemical cue has proved necessary. Some nudibranch species require only this chemical cue (Thompson, 1958; Hadfield and Karlson, 1969), while others also require contact with the prey species (Thompson, 1962; Tardy, 1962b). The prey substance initiating metamorphosis appears to be proteinaceous (Tardy, 1962b) and may be associated with the mucus of the prey (Hadfield and Karlson, 1969).

Two general nudibranch life cycle groupings have been proposed by Miller (1962) and Thompson (1964). The first contains nudibranchs which are short-lived, seasonal and feed on fast-growing, seasonal prey such as hydroids (Rasmussen, 1944; Swennen, 1961; and Tardy, 1962a and b). The second group is long-lived with annul life cycles and tends to feed on slow-growing, long-lived prey such as anthozoans and sponges (Thompson, 1958, 1961b and 1962; Swennen, 1961 and Potts, 1970).

Materials and Methods

All stages of the life cycle of *Phestilla melanobranchia* and *P. sibogae* were observed in the laboratory. Rearing of the veliger stage was attempted only at

the Hawaii Institute of Marine Biology, while observations on adult stages were made both in Hawaii (October 1966 to June 1967 and October 1968 to March 1969) and at the University of Singapore (September 1967 to June 1968).

Embryology of Phestilla melanobranchia

Mature specimens of both species of *Phestilla* deposit one or two egg masses per day for up to three months. To observe the embryology of *Phestilla melanobranchia* ten egg masses were isolated within an hour of deposition and maintained at 22° C in filtered sea water changed daily.

Small pieces of each egg mass were isolated in depression slides and observed at regular hourly intervals for the first three days, and then once or twice daily thereafter until all egg masses had begun to hatch. The water in the depression slides was changed every two to five hours, and new pieces of egg mass were used in each 24-hour observation period. After each new stage of development, a piece of corresponding egg ribbon was cut off and preserved in FAA (formalin, ethanol and glacial acetic acid in sea water).

Veliger cultivation

The techniques used for culturing veligers were adapted from those of Loosanoff and Davis (1963), and Struhsaker and Costlow (1968). Egg masses were placed in 10 cm diameter stacking dishes, and veligers were allowed either to hatch naturally or egg masses were artificially opened. All manipulation of veligers was accomplished by use of breath-controlled, finely-drawn glass pipettes. Transfer of the photospositive veligers was done in a darkened room with the beaker on a black background and a light source on one side. The veligers congregated on the lighted side where they could be collected and counted easily.

Veligers were cultured in 250 ml beakers containing 200 ml of water. The water was filtered through a styrofoam "Cuno" filter and changed daily.

Two cultured algae were used as food sources. The diatom *Phaeodactylum tricornutum* was used in all experiments and the green flagellate *Dunaliella* sp. was combined with *P. tricornutum* in a few cases. Five to 15 ml of algal culture were added daily.

The antibiotic penicillin was tested in several experiments to suppress bacterial growth in the cultures. The concentration of penicillin was 0.5–1.0 units/ml of culture medium.

Two techniques prevented the photopositive veligers from being trapped in the surface tension. In all experiments dark covers were placed over the upper half of the beakers so that light did not come from above. In later experiments, a few small cetyl alcohol flakes were sprinkled on the surface to reduce the surface tension, making the veliger shells less hydrophobic (Hurst, 1967).

In the first series of experiments (February to June 1967) temperatures of 25 to 27° C proved to be the most effective for veliger maintenance, but during the second series (October 1968 to February 1969), available laboratory facilities necessitated culturing at 21° C.

Small pieces of coral were added to the culture beakers to induce metamorphosis of the veligers. Small whole polyps of *Tubastraea aurea* were initially used for

Phestilla melanobranchia veligers, but pieces of skeleton and tissue taken from polyps of *Dendrophyllia elegans* were more effective and were used in most experiments. Small pieces of *Porites* colonies were used to induce metamorphosis in *Phestilla sibogae* veligers. I found that specimens of both *P. melanobranchia* and *P. sibogae* were best left undisturbed once settling had begun and so did not change the water in the beakers for several days after introducing the coral. When all veligers had completed metamorphosis, they were transferred with the original pieces of coral into 10 cm diameter stacking dishes. When the nudibranchs were 2–5 mm long they were moved to one of the systems used for adult animals.

Maintenance of adult nudibranchs

The two species of *Phestilla* were kept in the laboratory by three separate methods: running seawater tables, aerated aquaria and individual bowls. In Hawaii, nudibranchs were left in running seawater tables in which corals were also kept. All of the species of ahermatypic dendrophylliid corals found in Hawaii, as well as hermatypic corals in the genera *Porites, Montipora, Fungia, Pocillipora, Cyphastrea, Pavona* and *Leptastrea,* were available for nudibranchs to feed on.

A running seawater system was not available in Singapore, so the corals used to feed *Phestilla melanobranchia* were kept in 20 l aquaria.

Nudibranchs were also maintained separately or in pairs in plastic dishes approximately 20 cm in diameter and 10 cm in height. The water was changed daily, and the nudibranchs were supplied with small colonies of coral for food. By keeping individual animals isolated for long periods of time, it was possible to collect information on different aspects of their biology such as life span, growth rates, fecundity, color changes, preferences for coral species and many behavioral patterns.

Results

Sexually mature specimens of *Phestilla melanobranchia* or *P. sibogae* maintained with fresh coral and sea water laid an average of 1.5 egg masses per day for up to 100 days. The egg mass of each species is a flattened ribbon attached in a circle along one edge so that it flares somewhat. The eggs are arranged in tightly folded rows, oriented perpendicularly to the long axis of the ribbon. There is only one egg per capsule and the dimensions for egg mass, capsule and egg for both species of *Phestilla* are given in Table I. Egg masses for *P. melanobranchia* contain from 1,000 to 4,000 eggs each, with an average of about 3,000. Eggs of *Phestilla sibogae* are slightly larger than those of *P. melanobranchia,* and the egg masses contain fewer eggs, usually less than 3,000.

Table I

Sizes of egg masses, eggs, and capsules, veliger shells and newly metamorphosed stage in millimeters.

Species	Egg mass		Mean egg		Mean egg diameter	Mean veliger shell length	Newly metamorphosed stage mean length
	Length	Width	Length	Width			
P. melanobranchia	12–25	4–6	0.23	0.148	0.115	0.20	0.225
P. sibogae	15–25	4–7	0.28	0.18	0.148	0.264	0.30

Phestilla melanobranchia

The embryonic development of *Phestilla melanobranchia* is similar to that described for the aeolid *Fiona marina* (Casteel, 1904) and *Aeolis* (= *Cuthona*) *concinna* (Pelseneer, 1911).

The landmark stages in the embryonic development of *P. melanobranchia* and the average cumulative times for 10 egg masses at 22° C are as follows: deposition—0 hours, appearance of polar bodies—1 hour, 2-cell stage—4 hours, 4-cell stage—5 hours, 8-cell stage—6 hours, 12-cell stage—7 hours, 16-cell stage—8 hours, blastula—16 hours, gastrulation—29–40 hours, first movement—88 hours, torsion—112 hours, hatching—136–160 hours.

The cleavage rate varied among egg masses, but within a single egg mass the early cleavages appeared to be synchronized. Pieces of egg mass removed from the main mass often had cleavage rates out of phase with the main mass, but within the removed pieces cleavages remained synchronous.

Torsion in *Phestilla* entails a distinct 180 degree turning of the head and foot with respect to the shell. The shell is oblong and inflated and corresponds to Type 2 described by Thompson (1961a). The veligers are ready to hatch about 20 hours after torsion or about five days after deposition.

Veligers normally rotate slowly in the egg capsules which are surrounded by a gelatinous matrix. Only when the matrix disintegrated and the egg capsules came directly in contact with sea water did the veligers become active; then they would escape in one to two minutes. Veligers were repeatedly observed grasping the thin, flexible capsule wall with the mouth. Shortly thereafter, the veligers would escape through a hole in the capsule wall which corresponded to the area contacted by the mouth. Hatching veligers do not have a radula.

External factors are important in breaking down the matrix of the egg mass. The matrix of egg masses collected immediately after deposition and kept in motionless filtered sea water did not break down. Egg masses collected in the field, or left in running sea water tables for several days, broke down; they were subjected to water movement and colonization by bacteria, protozoans, nematodes, annelids and crustaceans. The fauna commonly associated with egg masses was not observed to attack developing veligers.

Phestilla melanobranchia veligers have little tissue inside the shell at hatching. They were very active and positively phototactic. Healthy, feeding *P. melanobranchia* veligers grew slowly until by the seventh day the body filled about two-thirds of the shell. The digestive gland was dark brownish-green from the *Phaeodactylum* pigments. No growth of the shell was observed after hatching. During this period, the foot thickened and by the eighth day, a propodium had formed and the veligers could crawl. When the veligers were ready to settle, they responded less to light, slowed their movement, and spent most of their time on the bottom. The velum appeared smaller and the color of the digestive gland faded, indicating a decrease in feeding.

Table II summarizes the results of culture experiments. In the one cultivation attempt where 13% of the veligers survived through metamorphosis, a motile green flagellate, *Dunaliella* species, was used in combination with *P. tricornutum*. Unfortunately, the *Dunaliella* cultures became contaminated with *Phaeodactylum* and were discarded thereby prohibiting further use of the alga.

TABLE II

Veliger cultivation results. Except where stated, the food source for veligers was the alga Phaeodactylum tricornutum.

Expt. number Date	Number beakers	Initial veliger	Veligers crawling	Metamorphosed	Percent metamorphosed	Coral species
Phestilla melanobranchia (Experiments 1–15 were unsuccessful and values given are average except where stated)						
Expt. 1–15	7	1403	0–1+[1]	0	0	*Tubastrea aurea* (expt. 1–4) *Dendrophyllia elegans* (expt. 5–15)
Expt. 16	2	400	4+	4	1.0	*D. elegans*
Expt. 17	2	400	0	0	0	*D. elegans*
Expt. 18[2]	2	800	many	107	13.4	*D. elegans*
Expt. 19	2	750	0	0	0	*D. elegans*
Expt. 20	2	1500	0	0	0	*D. elegans*
Phestilla sibogae						
Expt. 1 28 Oct. '68	1	125	many	67	53.6	*Porites compressa*
Expt. 2 30 Nov. '68	1	200	30	30	15.0	*P. compressa*
Expt. 3 7 Jan. '69	1	200	many	60	30.0	*P. compressa*
Expt. 4a	1	315	many	124	39.4	*P. compressa*
Expt. 4b 17 Feb. '69	1	350	many	12	3.4	*P. compressa*[3]

[1] One or more crawling veligers seen in eight out of 15 experiments.
[2] The alga *Duneliella* was used in combination with *P. tricornutum.*
[3] *Porites compressa* skeleton for two days and then live *P. compressa.*

Cetyl alcohol was very effective in keeping the shells of the veligers from becoming trapped in the surface film. When no cetyl alcohol was used, up to 100 out of 300 veligers might become caught in the surface tension between changes, whereas less than 25 would be trapped when it was used. Trapped veligers invariably accumulated material on their shells and tended to become attached to the bacterial film on the bottom where they were susceptible to bacterial and ciliate invasion.

Veliger density affected survival. Mortality was less at the concentration of 150 to 200 veligers per 100 ml than at 50 to 100 veligers. Bacterial activity seemed to be suppressed in the more crowded cultures.

Living coral tissue triggers settling and metamorphosis in *P. melanobranchia.* Small pieces of living *Dendrophyllia elegans* polyps were particularly effective for *P. melanobranchia.* Veligers could not settle directly on the tissue, and they were eaten if they encountered the tentacles of a whole polyp. Therefore, small pieces of skeleton and tissue were used. Such coral fragments lived for long periods if the water was changed regularly.

Once the *P. melanobranchia* veligers had settled on the skeleton near the tissue, the velum regressed quickly and disappeared in about 24 hours. The digestive

gland lost all color and the body came free of the shell within 24 to 48 hours. The small nudibranchs became vermiform in shape within 24 hours after dropping their shells. Feeding began shortly thereafter and was indicated by the yellow and red coloration of the digestive gland. The buds of the first cerata also appeared at this time.

In *P. melanobranchia,* the most critical period for successful cultivation was that following the addition of coral. Crawling veligers were observed in eight of the first 15 culture attempts with *P. melanobranchia,* but in each case attempts to isolate these animals were either unsuccessful or the experiment was terminated too soon after the coral was added. Had the cultures been left alone after the addition of coral, successful metamorphosis would likely have been a far more regular occurrence.

The results of growth rate measurements are summarized in Table III. The percent increase in body length was greatest in small animals and dropped off with size. There was a distinct drop in growth rate at a length of about 20 mm, which corresponded to the onset of egg mass production. The maximum length attained in the laboratory was approximately 40 mm; specimens of comparable length were collected in the field. *P. melanobranchia* was recorded from egg to egg in 60 days and the maximum life span was over 140 days.

In *P. melanobranchia* the male system is functional by the time the nudibranchs reach 10 mm in length. The female system becomes functional when they reach 20 mm as indicated by egg mass production. If a nudibranch has mated with another animal 10 mm or larger, then the eggs are fertile and they will develop. If the nudibranch has not mated, no development takes place. Egg masses from mated nudibranchs are 100% fertilized. Specimens of *P. melanobranchia* receive enough sperm from a single mating to last for more than two weeks of continuous laying.

A summary of egg mass production is presented in Table IV. Egg mass production was continuous for the greater part of the life span with an average

TABLE III]

Summary of growth rate data in millimeters per day and percent increase per day, from Harris, 1973.

	0.2*–5 mm	5–10 mm	10–15 mm	15–20 mm	20–25 mm	25–30 + mm
Phestilla melanobranchia						
Hawaii						
Average	0.34	0.50	0.86	1.27	1.00	0.79
% Increase	12.25	6.27	6.41	6.76	4.27	2.79
Singapore						
Average	0.27	0.41	0.82	0.62	0.73	0.62
% Increase	9.78	5.13	6.15	3.39	3.03	2.20
Phestilla sibogae						
Hawaii						
Generations F_{1-3}						
Average	0.46	0.62	0.94	1.30	0.83	0.69
% Increase	15.47	7.64	7.60	6.91	3.54	2.44

* Length immediately after metamorphosis.

TABLE IV

Fecundity and life span/data.

	Number nudibranchs in sample	Mean maximum number egg masses per day	Mean number egg masses per day	Mean minimum number egg masses per day	Maximum total egg masses (number days)	Life span in laboratory
Phestilla melanobranchia						
Singapore	41	2.72	1.82	0.16	140 (76)	86 days 17 mm*
Hawaii	48	2.63	1.53	0.76	152 (118)	135 days 8 mm*
Phestilla sibogae						
Hawaii Field	3	1.55	1.52	1.50	175 (117)	122 days**
Hawaii Lab. F_1	10	1.94	1.57	1.14	178.5 (114)	139 days†
Hawaii Lab. F_2	8	1.79	1.45	1.00	113 (83)	114 days†
Hawaii Lab. F_3	10	2.06	1.71	1.31	101 (53)	84 days**†
Hawaii Lab. F_4	10	2.33	2.08	1.70	22 (10)	43 days**†

* = nudibranch size when collected.
** = terminated early.
† = from hatching as veliger.

of more than 1.5 egg masses being laid each day; this was consistent as long as adequate food and clean sea water was provided. Young individuals produced an average of nearly two egg masses per day and the average daily production decreased as the animals grew older.

Removal of food stimulated an increased egg mass production for a few days and return of coral caused cessation of egg mass laying for a day or two before normal production resumed.

Phestilla sibogae

Development of *P. sibogae* to the veliger stage is identical to that of *P. melanobranchia.*

Hatching *P. sibogae* veligers, which are lecithotrophic, look very much like *P. melanobranchia* veligers that have been feeding for seven days; the shell is filled with tissue though the digestive gland has no color. *P. sibogae* veligers were inactive for two days and spent much time on the bottom. They fed little or not at all, and the digestive gland did not turn dark. By the third day, the veligers had developed a propodium on the foot and crawled and swam alternately. They were markedly more active than on the two preceding days, and swam quickly toward a light source placed to one side of the beaker.

Living *Porites* tissue added on the third day induces *P. sibogae* veligers to metamorphose within 24 hours (see Table II). *P. sibogae* settles directly on

Porites tissue as well as anywhere in the beaker, as long as coral is present. One *P. sibogae* veliger was observed to metamorphose in the absence of any coral tissue, but this was one out of 300 veligers.

Both species settled at relatively specific times, three to four days after hatching for *P. sibogae* and eight to ten days for *P. melanobranchia*. *P. sibogae* veligers began to die if they did not hatch in eight days, and five days following hatching the majority of the veligers would not respond to live *Porites* tissue.

After metamorphosis, *P. sibogae* had a higher percent increase in body length than did *P. melanobranchia* and the growth rate slowed in both species at a body length of about 20 mm which corresponds to the onset of egg mass production (see Table III). Both *Phestilla* species attained a maximum length of approximately 40 mm in the laboratory.

The fecundity of *P. sibogae* was similar to that of *P. melanobranchia,* with individuals of both species producing about one and a half egg masses per day (see Table IV). A comparison of the *P. sibogae* F_1 and F_2 generation production data with that of the prematurely terminated F_3 and F_4 generations clearly demonstrates the decrease in egg mass production with time.

A faster growth rate shown by *P. sibogae* combined with the shorter period from hatching to metamorphosis explain the differences in generation time between the two species. *P. melanobranchia* was cycled from egg to egg in 60 days, while *P. sibogae* averaged 38 days over four generations. The maximum life span for each *Phestilla* species was approximately 140 days, though *P. melanobranchia* may exceed this by two or three weeks.

P. melanobranchia was more sensitive to crowding and water fouling than *P. sibogae*. *P. melanobranchia* maintained alone or paired on *Tubastraea aurea* or *Dendrophyllia elegans* generally did very well. Survival of *P. melanobranchia* in groups of more than two was markedly reduced. *P. sibogae* was much hardier under crowded conditions and closely packed aggregations of over 100 adults were common in the running seawater table where a large population was maintained.

The water from Kaneohe Bay, Hawaii, had a high organic content, and on several occasions, the water became foul in less than 24 hours. *P. sibogae* proved to be quite resistant to this fouling, but *P. melanobranchia* was not able to tolerate it and twice most of the *P. melanobranchia* being maintained in bowls were killed.

Discussion

Serial culture of an animal in the laboratory opens a broad vista of studies for which it may be utilized. *Phestilla sibogae,* whose initial cultivation in 1969 is described here, is still under cultivation (Hadfield and Karlson, 1969; Bonar, 1973; Bonar and Hadfield, 1974). Also, knowledge of the complete life cycle of an animal provides important insights into its biology. While the life histories of the two *Phestilla* species are similar, they show differences which can be linked to the biology of their respective coral prey. The differences between the two species, and from other aeolids reported in the literature, will be discussed below.

The embryology of *Phestilla* follows the general pattern reported for other nudibranch species (Casteel, 1904; Pelseneer, 1911). The complete development

of *Phestilla* from newly laid egg to hatching veliger takes five to seven days at 21–25° C. Developmental times of a number of aeolid species reported in the literature are similar to this (Hadfield, 1963).

Observations on the embryology of *P. melanobranchia* suggest that some mechanism synchronizes early cleavage within an egg mass. Such a mechanism could act as a pace setter which would insure completion of development for most of the veligers before the egg mass begins to deteriorate. It also suggests possible chemical mediation within the egg mass.

The consistent observation that veligers are dependent on external factors to erode the gelatinous matrix of the egg mass is surprising. Observations on the egg mass of other species suggest that this may be a general phenomenon among nudibranchs. Important factors in this breakdown appear to be water movement, bacterial degradation and burrowing by small animals such as nematodes and annelids.

An important problem in rearing the veligers of *P. melanobranchia* was keeping the food supply in suspension. Shaker tables were tried but veliger entrapment by surface tensions made this method impossible. A constant food source would increase the growth rate, perhaps resulting in a reduced cultivation time, and increased survival. The highest survival rates for *P. melanobranchia* occurred when the motile alga *Dunaliella* sp. was used in combination with *Phaeodactylum*. Unfortunately the *Dunaliella* cultures were lost before it was possible to exploit them further.

Living coral tissue is necessary to induce settling and metamorphosis in both species of *Phestilla*. Hadfield and Karlson (1969) found that some proteinaceous factor in *Porites* mucus is responsible for inducing metamorphosis in *P. sibogae*. A similar mechanism is likely to be responsible for metamorphosis in *P. melanobranchia*.

P. melanobranchia veligers were observed to undergo metamorphosis only in close proximity to the coral tissue, though not on it. *P. sibogae* veligers underwent metamorphosis anywhere in the beaker if coral was present. Therefore, while a chemical cue from living prey is necessary for inducement of settling and metamorphosis in nudibranchs, actual contact with the prey is not a consistent requirement (Harris, 1973).

The settling-related behavior of *Phestilla* veligers correlates well with the ecology of their respective coral prey. *Porites* corals are large, photopositively distributed and extremely common in Hawaii. Veligers of *P. sibogae* become positively phototactic when ready to settle and will settle on or in the vicinity of the coral tissue. Dendrophylliid corals are photonegatively distributed, small and patchy in distribution. Veligers of *P. melanobranchia* become negatively phototactic when ready to settle and must be in close proximity to the coral. Dendrophylliid corals will eat *P. melanobranchia* veligers, and the veligers can only settle adjacent to the tissue of the coral.

After hatching, *P. sibogae* grows faster than *P. melanobranchia* at each stage up to the adult size of about 40 mm. *P. sibogae* is ready to settle in three days and completes metamorphosis in one day more, while *P. melanobranchia* takes eight and three days respectively. After metamorphosis, *P. sibogae* reaches sexual maturity approximately two weeks sooner than *P. melanobranchia* and the maxi-

mum life spans of over four months are similar. A possible explanation for the difference in growth rate may be nutritional adaptation to the prey. *Phestilla sibogae* may utilize *Porites* tissue more effectively than *P. melanobranchia* utilizes dendrophylliid tissues. *Porites* contains zooxanthellae which *P. sibogae* digests. In addition, zooxanthellae continue to photosynthesize for several days in the digestive gland of *P. sibogae* (L. Muscatine, personal communication, 1969, University of California, Los Angeles). The role of zooxanthellae in the nutrition of *P. sibogae* and the comparative energetics of these two nudibranch associations would be rewarding areas of further study.

Both *Phestilla* species begin laying egg masses when they are about 20 mm in length and continue to spawn and feed for about 100 days. There is no interruption of feeding such as has been found in some seasonal species on the coast of England. Thompson (1958, 1961b) reported that several dorid species stop feeding when they begin spawning and actually starve to death before they deplete their reproductive capabilities. Most aeolids described in the literature and observed by the author continue to feed and spawn for considerable periods (Rasmussen, 1944; Tardy, 1962a and b). Individuals of both species of *Phestilla* survived for more than a week after they ceased laying and the gonads were depleted; during this time they fed and continued to associate closely with their mates.

Several generations of each *Phestilla* species are produced in a year, placing them in Miller's (1962) Group 2. The numbers of *Phestilla melanobranchia* did not vary greatly during different times of the year, and the number of nudibranchs in a given area depended on the concentration of dendrophylliid corals available. The species of nudibranchs listed by Miller (1962) and Thompson (1964), which have several generations a year, generally feed on fast growing, seasonal prey. The prey of both species of *Phestilla* is stable and slow growing, so they might be expected to live longer than the observed maximum of four and a half months. *Phestilla* is a member of the Family Cuthonidae, other species of which are small, fast-growing hydroid eaters; thus the growth rates of the *Phestilla* species may be more influenced by their genetic background than the stability of the food source.

Predation on nudibranchs may be another factor influencing longevity. To grow fast and reproduce as rapidly as possible before being eaten may be far more important than the availability of the food source. Differences between generation time of the two species of *Phestilla* may also be influenced by predation pressures.

P. sibogae is more susceptible to predation than *P. melanobranchia* and this pressure could in time have selected for faster growth. Pressure from predation combined with the great abundance of *Porites* could have led to lecithotropic development thereby minimizing exposure of the veliger stage to predation (Thorson, 1946). In contrast, the patchy distribution of dendrophylliid corals could tend to select for a longer veliger stage thereby providing more dispersal time in *P. melanobranchia*.

In conclusion, the differences in life cycles of *P. melanobranchia* and *P. sibogae* can be related to the biology of corals. Harris (1970) also found that pigmentation, morphology and adult behavior all reflect characteristics of the prey. The differences in generation time between *Phestilla* and other nudibranchs with stable prey popula-

tions is likely to be related to adaptations to avoid predation and/or the affinities of *Phestilla* with the Family Cuthonidae.

It is the author's belief that many nudibranch species could be cultivated successfully if one were willing to devote the time necessary to work with the veliger stage and the prey species. Knowledge of the biology of the prey greatly facilitates the study of any nudibranch species.

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Summary

1. The complete life cycles of two coral-eating aeolid nudibranchs, *Phestilla melanobranchia* Bergh, 1874 and *Phestilla sibogae* Bergh, 1905, are described. Information on their life histories includes developmental stages and timing, duration of the veliger stage, veliger behavior, factors necessary for settling and metamorphosis, and adult growth rates, fecundity and longevity. The life cycles of the two *Phestilla* are similar and their physical and behavioral differences are related to the characteristics of their respective coral prey.

2. *P. melanobranchia* has planktotrophic development, is negatively phototactic when ready to settle, requires close proximity to living dendrophylliid coral tissue for metamorphosis and has a generation time from egg to egg of 60 days. The dendrophylliid corals on which *P. melanobranchia* feeds are small, patchy and photonegative in distribution.

3. *P. sibogae* which has now been under serial cultivation for four years, has lecithotrophic development, is positively phototactic when ready to settle, requires only a chemical factor from living *Porites* tissue for metamorphosing and has a generation time of 38 days. The *Porites* corals which *P. sibogae* feeds on are large, very common and photopositive in distribution.

4. Differences in predation pressure and prey tissue utilization efficiency are proposed as factors influencing the evolution of a significantly faster generation time in *Phestilla sibogae* than in the closely related *P. melanobranchia*.

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